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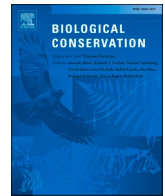
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Policy analysis

Increasing protected area coverage mitigates climate-driven community changes

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ABSTRACT

Climate change has ubiquitous impacts on ecosystems and threatens biodiversity globally. One of the most recognized impacts are redistributions of species, a process which can be hindered by habitat degradation. Protected areas (PAs) have been shown to be beneficial for preserving and reallocating species occurrences under climate change. Yet, studies investigating effects of PA networks on species' range shifts under climate change remain scarce. In theory, a well-connected network of PAs should promote population persistence under climate change and habitat degradation. To study this, we evaluated the effects of PA coverage on avian communities in Finland between two study periods of 1980–1999 and 2000–2015. Climate-driven community impacts were investigated by using community temperature index (CTI). We used linear models to study the association of PA coverage and the CTI changes in southern, central and northern Finland. In northern and central Finland, higher PA coverage was associated with lower changes in CTI and 45% PA coverage in northern and 13% in central Finland corresponded with complete mitigation of CTI increase. These results indicate that higher PA coverage strongly increases community resilience to warming climate. However a similar association between PA coverage and changes in CTI was not apparent in southern Finland. The PA coverage in southern Finland was much lower than in the two other sections and thus, may be too sparse to favour community resilience against climate change. The results provide empirical evidence for the international need to rapidly expand PA networks and halt biodiversity loss.

1. Introduction

Human induced climate change is projected to markedly damage global biodiversity (Bellard et al., 2012; IPBES, 2019) and none of the ecosystems on Earth have remained unaffected (Scheffers et al., 2016). Together with habitat loss and degradation, the effects of climate change can be devastating (Oliver et al., 2017; Travis, 2003) leading to species and population extinctions (Jackson and Sax, 2010). One of the most recognized effects of climate change is the redistribution of species as a consequence of altered climatic conditions (Bonebrake et al., 2018; Chen et al., 2011; Thuiller et al., 2005).

Within degraded and fragmented habitats, species may have restricted possibilities to persist and trace their preferred climatic

conditions (Ash et al., 2017; Parmesan, 2006; Robillard et al., 2015). Therefore, the synergistic impacts of anthropogenic climate and habitat changes are triggering a marked turnover in the composition and functional diversity of wildlife communities (Lawler et al., 2009; Virkkala and Lehtikoinen, 2017). This may lead to functional homogenization due to loss of specialist species (Thuiller et al., 2014).

Protected areas (hereafter PAs) are the cornerstones of nature conservation, ensuring species and habitat persistence (Watson et al., 2014). Although the performance of the conventional static network of PAs to protect species under the dynamic and asymmetrical process of climate change has been questioned (Ferro et al., 2014; Monzón et al., 2011), a large body of evidence supports the ability of PAs to preserve biodiversity under global warming (Gillingham et al., 2015a; Johnston et al.,

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2013; Lehtikoinen et al., 2019). PAs have been shown to facilitate species distribution expansions (Thomas et al., 2012) especially when effectively managed (Lawson et al., 2014), but also to mitigate species retractions on the trailing range edges of distributions (Gillingham et al., 2015b; Lehtikoinen et al., 2019). Furthermore, evidence suggests that PAs are able to protect threatened species under climate change (Thomas and Gillingham, 2015). This is especially relevant because the detrimental effects of climate change disproportionately impact already threatened species (Massimino et al., 2017). Ultimately, biological communities occurring within PAs may be more resilient to climate-driven changes as compared to communities occurring on unprotected land under multiple stressors (Gillingham et al., 2015a; Olds et al., 2014; Santangeli et al., 2017).

So far, species distribution models (SDMs) have represented the backbone of studies addressing the impacts of predicted climate change on biodiversity and showing the strengths and weaknesses of the current PA network (Araújo et al., 2011; Araújo and Peterson, 2012; Heikkinen et al., 2006). SDMs model associations between the occurrence of species and climate, among other factors, and enable quantification of suitable conditions for existing populations. SDMs can be further used to model future suitable conditions and occurrence probabilities based on climatic trajectories (Araújo and Peterson, 2012). Many studies have therefore concentrated on projecting future impacts, but the evidence on current impacts of climate change on species are also direly needed for the validation and improvement of such projections (Pacifi et al., 2017). Most studies concerning species distribution changes under climate change are based on occurrence data and ignore climate-induced shifts in abundances (Virkkala and Lehtikoinen, 2014). Recent evidence shows that abundance data increase the reliability in generating outcomes for conservation prioritization (Howard et al., 2014; Johnston et al., 2015). Whereas the body of evidence on species vulnerabilities to climate change is ever increasing (Foden et al., 2019), the features of PAs that contribute to successfully mitigating such vulnerabilities remain less known (Sieck et al., 2011).

In addition to climatic conditions, the landscape composition and structure surrounding PAs plays a crucial role for the redistribution of wildlife under climate change (Virkkala et al., 2019). Intensified land use may diminish the amount and/or quality of natural habitat surrounding PAs in the future (Gimona et al., 2012; Martinuzzi et al., 2015), emphasizing the key role of PAs in preserving high quality habitats (Fraixedas et al., 2017). A landscape that facilitates movement from one PA to another increases the connectivity of PAs and the capacity of the network in buffering against climate change (Keeley et al., 2018; Santini et al., 2016). An important next step in improving the reliability of projected impacts of climate change is to unravel the complexities of how PA coverage and quality can interact with a landscape structure outside PAs to define the ability of the entire PA network to mitigate or diminish negative impacts of climate change (Keeley et al., 2018; Reside et al., 2018).

The composition and quality of habitats surrounding PAs thus can have a major effect on biodiversity persistence. According to metapopulation theory, a population is more likely to persist in a large and well-connected patch of habitat than in a small and fragmented one (Hanski, 1998; Harrison, 1991). This is because the species' ability to move between habitat patches is enhanced in well-connected landscapes (Hanski, 1999), and because larger patches hold larger population sizes than smaller ones (Hanski, 1998). Therefore, a well-connected network of habitat patches enhances the persistence of both metapopulations and biodiversity (Hanski, 1998). High coverage of habitat patches is also likely to increase the heterogeneity of landscapes. This enhances climatic resilience and spreads the risk of local extinctions between patches under extreme weather events (Piha et al., 2007; Sutcliffe et al., 1997). Therefore, a well-connected network of PAs more likely allows populations to persist under spatial dynamics of climate change and habitat degradation (Hannah, 2008) and this factor is widely integrated in the spatial planning of PA networks (Keeley et al., 2018; Santini et al.,

2016).

Here we studied the effects of PA coverage and forest cover on changes in avian communities within Finnish PAs between two time periods (hereafter periods): 1980–1999 and 2000–2015. We used community temperature index (hereafter CTI; Devictor et al., 2008) to investigate climate-driven impacts on Finnish land bird communities, which were sampled with line transects in 181 PAs throughout the country. CTI is a simple and generalizable indicator representing community weighted mean of species' temperature preference, and is commonly used to study climate-driven temporal shifts in both marine and terrestrial communities (Devictor et al., 2012; Flanagan et al., 2019; Santangeli et al., 2017). Climate induced range shifts typically manifest themselves in a fixed location as decreases in cold-dwelling and increases in warm-dwelling species, overall leading to increased CTI values (Devictor et al., 2012; Santangeli et al., 2017). We predicted that the higher the PA network coverage the more effective it was in mitigating climate-driven changes in avian communities (measured as Δ CTI between the two periods). We based this prediction on previous studies, which have shown that i) intense land use in the landscape matrix between PAs hampers the persistence of species assemblies (Häkkinen et al., 2017) and that ii) larger PAs are able to alleviate changes in CTI (Santangeli et al., 2017).

The number and, especially, the mean size of PAs are the main drivers of the connectivity of PAs in any given ecoregion (Santini et al., 2016; Saura et al., 2017). Conversely, dispersal distances contribute less to predicting the amount of reachable habitat for terrestrial vertebrates in PA networks (Santini et al., 2016; Saura et al., 2017). Therefore, the studied PA coverage within the Finnish Boreal ecoregion corresponds roughly to PA connectivity, especially when studying an assemblage of species where dispersal distances vary widely between species (Santini et al., 2016; Saura et al., 2017). Last, we examined if the potential link between CTI change and PA coverage was caused by population changes of either warm- or cold-dwelling species, or both. Our prediction was that cold-dwelling species would have a higher contribution to CTI changes. This prediction was based on a previous study showing that under climate change driven redistribution processes, PAs mitigate declines of a wide range of retracting cold-dwelling species but facilitate expansions of only a few warm-dwelling bird species (Lehtikoinen et al., 2019).

2. Materials & methods

2.1. Line transect data

To derive a CTI value for each PA and each of the two periods, we used abundance data collected in the Finnish land bird line transect scheme conducted from 1980 to 2015 in a total of 181 PAs (Santangeli et al., 2017). Altogether the line transects accounted for 171 bird species belonging to 16 genera (Table S1). Line transect methodology is appropriate to obtain robust relative abundances of species over large areas because it provides simple and time-efficient means to cover long distances and to achieve large sample sizes (Bibby et al., 2000; Lehtikoinen and Virkkala, 2016). Transect routes were preset and usually spanned 3–6 km which is a reasonable length to cover in one morning before the reduction in singing activity of the birds. The transect locations were selected so that they covered habitats corresponding to habitat availability in a given PA (Santangeli et al., 2017). The amount of transect kilometres corresponded to the size of a given PA. Therefore larger PAs had more than one transect making the PA – and not the transect – the sample unit. Transects were surveyed during the breeding season in a single visit by walking at a moderate pace (ca. 1 km/45 min), but were not necessarily repeated every year. The survey period ranged from the 21st of May to the 20th of June in southern Finland and from the 10th to the 30th of June in northern Finland. In the northernmost montane parts of the country surveying continued until the 5th of July. The differing surveying times at the different latitudes are due to the

later onset of spring and thus later bird breeding at higher latitudes. Moreover, the transect season was timed in each section to the main breeding season of birds and after the migration season to prevent migrants to be included in the transect counts. The relative number of migratory species increases with increasing latitude (Newton and Dale, 1996a, 1996b) and the Finnish bird community comprises relatively few resident species. Despite a few resident species and short-distance migrants breed earlier than the long-distance migrants, the timing of transect season in early summer ensures that all the migratory species have arrived at their breeding grounds while the residents are still amidst their breeding season.

Transects were surveyed in the early morning under weather conditions favourable for detection of birds. All bird individuals were documented and classified according to whether they were singing, calling, flying and/or nesting. In addition, the sex, age and brood and flock-size were recorded when applicable. Based on this information, all observations were transformed into number of pairs, which is the survey unit (e.g. a singing male = 1 pair; Lehtikoinen et al., 2019). Observations included only individuals which were identified to species level with the exception of crossbill species (*Loxia sp*) which are difficult to identify based on the vocalization alone but form a notable contribution among observations (Table S1).

The locations of all the individuals observed along the transect were documented in either to the main belt spanning 25 m on both sides of the surveyor or exterior to this main belt (Järvinen and Väisänen, 1975). The ratio of observations inside and outside of 50 m wide main belt was calculated from the data of PAs in all sections and on both periods for all the 171 studied species (Järvinen and Väisänen, 1975). This ratio was used as species-specific detectability coefficients (Järvinen and Väisänen, 1975; Lehtikoinen and Virkkala, 2016). An exception was made in black grouse (*Lyrurus tetrix*) since the singing activity and thus detectability of the species decreased notably during the survey period (Lehtikoinen, 2013). Therefore, for this species a detectability coefficient was calculated separately to two time periods, which were before and after the 15th of June. The relative density of each species was calculated by multiplying the observed number of pairs per transect kilometre with a species-specific detectability coefficient (Lehtikoinen and Virkkala, 2016). The detectability coefficient was used to avoid the overrepresentation of easily detectable species (e.g. loud and visible species) and the underrepresentation of species difficult to detect (e.g. elusive, small and relatively silent species), which may lead to biased conclusions regarding the composition of the bird community (Johnston et al., 2015). The line transects within a PA covered on average (\pm SD) 37 ± 53 km on the first period and 40 ± 57 km on the second period. The total lengths of transects were 1010 km and 1009 km in southern, 2243 km and 2185 km in central and 3597 km and 4453 km in northern Finland in the first and second period, respectively. The differences in the amount of transect kilometres between the periods derive from unequal period lengths and from the fact that transects were not necessarily conducted every year. However, the relative densities studied were not affected by the differences in transect lengths between periods.

2.2. Community temperature index (CTI)

We used the relative densities of the land bird species encountered on the line transects to generate CTI values for each PA in the two time periods of 1980–1999 and 2000–2015. The CTI values were generated by first obtaining species temperature index (STI) for each of the species considered. The STI was calculated as the average of the monthly average temperatures of March–August in years 1950–2000 across the breeding range of the species in the whole of Europe (Devictor et al., 2008). The species distribution data were obtained from EBCC atlas of European breeding birds (Hagemeijer and Blair, 1997) and the temperature data from WORLDCLIM database (www.worldclim.org). The methodology of the temperature data has been described by Hijmans et al. (2005). A mean STI between common (*Loxia curvirostra*) and parrot

crossbill (*L. pytyopsittacus*) – the two common crossbill species in Finland – was used for representing STI of the unidentified crossbills. The obtained STIs represent the spatial association of a given species to certain temperatures and are the basis for generating CTIs (Devictor et al., 2008). The CTIs for both periods within a PA were calculated by weighting all the STIs with the mean annual relative densities of the given species in that period and PA, and finally averaging across density weighted STIs of all the species in a given period and PA (Devictor et al., 2008; Lindström et al., 2013). Thereby, the CTIs represent the average breeding season (March–August) temperature preference of a bird individual in the community. The change in CTI between the two periods (hereafter Δ CTI) for each PA was then calculated by subtracting the CTI of the first period (1980–1999) from the CTI of the second period (2000–2015). A positive change in CTI means that the community has moved towards species preferring warmer conditions, whereas negative change represents a move towards species preferring colder conditions.

2.3. Characteristics of protected areas

The coverage of PAs in Finland is not homogeneously distributed, but rather spatially biased, with larger PAs concentrated towards the northern part of the country (Fig. 1). To avoid spatial autocorrelation deriving from this non-random pattern, we studied three latitudinal sections of Finland (hereafter sections) separately. These sections were i) southern Finland (latitudes up to $63^{\circ}04'57''$ N; Finnish uniform coordinate system 700), ii) central Finland ($63^{\circ}04'57''$ N – $65^{\circ}46'15''$ N; 700–730) and iii) northern Finland ($65^{\circ}46'15''$ N northwards; >730) (Fig. 1). In total we studied 181 PAs, out of which 49 were located in the southern, 74 in the central and 58 in the northern section (Fig. 1a). We then calculated the size of each studied PA using GIS tools in the software ArcGIS 10.3 (ESRI, 2019). We calculated the proportion of land covered by PAs (hereafter PA coverage) within circles with radii of 25 km, 50 km and 100 km centred in the centroid of each PA. These radii were used because they cover the median dispersal abilities of the majority of the bird species (Santini et al., 2016; Saura et al., 2017; Sutherland et al., 2000). When calculating the PA coverages we included the coverage of the focal PA itself as well as all other PAs within the certain radius considering PAs in Finland and neighbouring countries when applicable. For counting the coverages, a public version of the World Database on Protected Areas was downloaded from Protected Planet (WPA, 2020). The PAs considered here all belonged to the IUCN PA categories I–IV (Dudley, 2008). The average PA size (\pm SD) was 15.2 ± 16.3 km² in the southern, 27.4 ± 38.7 km² in the central and 357.9 ± 681.7 km² in the northern section. The mean PA coverage was lower with increasing radius in all sections and spanned 2.2–2.8% in the southern, 5.6–7.3% in the central and 23.0–29.8% in the northern section.

As a measure of habitat availability, we calculated a forest cover index for each PA. This index was derived from the proportion of open versus forested land within each PA. The forest cover index values ranged from 0 to 1, where extreme values corresponded with the PA being totally open or totally forested, respectively. A given land area was classified as forest land if the annual mean wood production rate (mean annual increment) was over 1 m³/ha, a value which is only reached in a dense tree cover (Natural Resource Institute Finland, 2012). The land area was classified as open land if the mean annual increment was <0.1 m³/ha, which in turn represents a value where only single trees might be present e.g. meadows, open mires and montane tundra. However, sparsely wooded land with low forest growth rate such as scrub land (mean annual increment: 0.1–1 m³/ha) can be suitable for both species that prefer forest and for those preferring open land. We therefore included such lands in both the forested and open land areas. The spatial data on mean annual increments were obtained from the database of Metsähallitus National Parks Finland (Metsähallitus, 2020). The mean (\pm SD) forest cover index was 0.72 ± 0.26 for the southern, 0.64 ± 0.22 for the central and 0.60 ± 0.23 for the northern section.

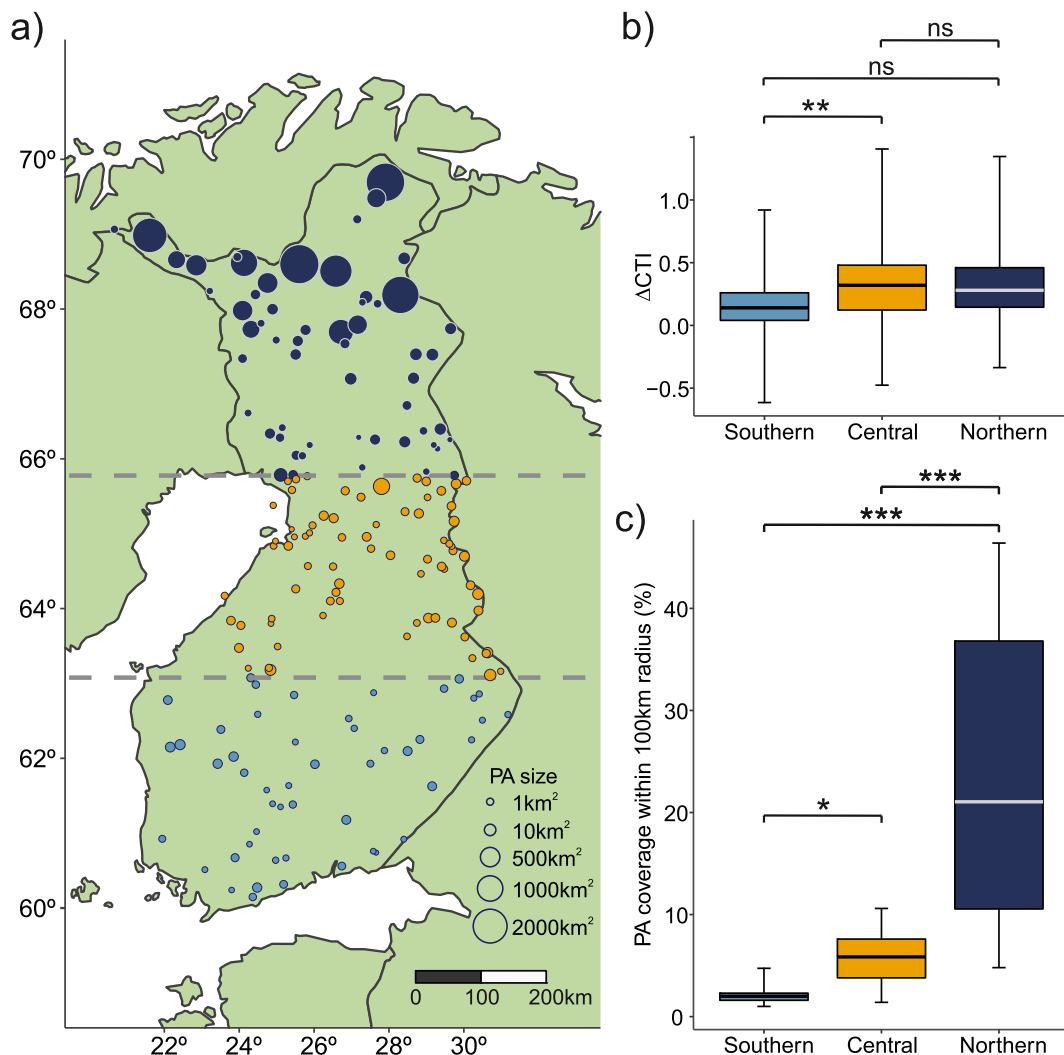


Fig. 1. Characteristics of the studied protected areas. Panel a shows the distribution and size of the protected areas included in this study. Light blue circles represent the protected areas in southern, yellow those in central and dark blue those in northern Finland, the dashed lines also delineate these sections. Panel b illustrates the changes in community temperature index between the two study periods (1980–1999 and 2000–2015) across each latitudinal section of the country. Panel c shows the distribution of protected area coverage within a 100 km radius from the centre of protected areas in the latitudinal sections. The whiskers represent the whole range of the data, midline the median value, and boxes the median 50% of the data. The statistical differences of Tukey post-hoc test between sections in 1b and 1c illustrated with symbols (ns = non-significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). [Fig. 1. in colour on online only]. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Finnish PAs mainly consist of boreal forests and peatlands, but in addition they protect threatened habitats including traditional rural landscapes, coastal habitats and shore meadows, montane birch forests and tundra (Raunio et al., 2008). Four fifths of the land cover in Finland is forested (EEA, 2015), out of which 12% is protected (Natural Resource Institute Finland, 2016). However, if scrub lands with low annual increment are excluded from the forested land, only 6.6% of the remaining forest lies within PAs (Natural Resource Institute Finland, 2016). Forestry is prohibited inside PAs and in general operated intensively outside PAs. Therefore, PAs typically support older and more heterogeneous age structure forests, as well as higher volumes of dead wood as compared to unprotected forest lands (Metsähallitus, 2019). Peatlands cover 28% of the Finnish land area and consist of both open mires (19%) and forested mires (81%). In total, 13% of the Finnish peatlands are found inside PAs. Over 60% of the peatlands present in Finland during the pre-industrial era have been drained for forestry purposes (Fraixedas et al., 2017), and therefore pristine and open mires are currently sporadic outside PAs, particularly in southern Finland. Major land use actions that may damage nature values are strictly

prohibited inside PAs. Therefore the characteristics of the studied PAs have hardly changed between the periods with the exception of climate-induced impacts (Virkkala et al., 2018).

2.4. Statistical analyses

To study changes in CTI we used linear regression models separately for southern, central and northern Finland. The response variable in all the models was Δ CTI for each PA between the two periods. The CTI in the first period was included as an explanatory variable to account for the initial community structure. Communities with lower initial CTIs may be predisposed to larger changes than communities with higher CTIs. To correct for the possible effect of the main habitat type in a PA on the Δ CTI, the forest cover index was included in the models as an explanatory variable. Many northern species are open landscape specialists and inhabit treeless mires and montane tundra. Because of this, the species composition may stay more similar in PAs with open landscape than in PAs mainly consisting of forest. Alternatively, the rapid habitat degradation of open landscapes under climate change may

hamper the persistence of these avian assemblages (Chamberlain et al., 2013; Virkkala and Rajasärkkä, 2012), which may reflect in increased changes in CTI in PAs with larger proportions of open than forested habitats. To assess the effect of PA coverage in different distances, we used as explanatory variables focal PA size or PA coverage within radii of 25 km, 50 km or 100 km, which cover the median dispersal abilities of the majority of the bird species (Santini et al., 2016; Saura et al., 2017; Sutherland et al., 2000). All the variables in the models were continuous, and collinearity among explanatory variables was assessed quantitatively by examining variance inflation factors (VIF). VIF values were calculated using function “corvif” (Zuur et al., 2009; Highland Statistics Ltd, 2020) in the R 3.5.3 software (R Core Development Team, 2019). Explanatory variables with large VIF values (>3) were not included in the same models due to collinearity (Zuur et al., 2007).

Since the size of the focal PA and both the smaller radii (25 km and 50 km) describing PA coverages are fully contained within the largest radius of 100 km, we used a pre-analysis selection process to discern which of these variables best explained Δ CTI in order to avoid multiple testing. In this process, we first built four competing models for each section. In these models Δ CTI was explained by forest cover index and one variable describing the amount of PA coverage (i.e. one of the three radii surrounding the centre point of the focal PA or the size of the focal PA itself) as well as the interaction between this variable and forest cover index. The four models for each section were then compared using Akaike's information criterion corrected for small sample size (AICc) (Akaike, 1974; Sugiura, 1978). CTI of the first period was also included in all models, except models explaining Δ CTI in southern Finland. We excluded CTI in the first period for the southern section because this variable showed strong collinearity with the forest cover index (VIF = 3.07–3.32, depending on the model). The model containing the 100 km radius surrounding the centre of the focal PA exhibited the lowest AICc values in northern, central and southern Finland (Tables S2–S4), and was chosen for the actual analyses in which we explored the factors influencing Δ CTI. The PA coverage within 100 km radius differed significantly between the three sections ($F_{2,178} = 113.7$, $p < 0.001$) and the post-hoc Tukey test revealed that all the sections differed statistically from each other (Fig. 1c).

To elucidate which variables affect Δ CTI in the different sections we built competing model sets for each section and implemented an information theoretical approach to evaluating the most influential variables. To that end, we built model sets for both northern and central section in which the most complex model contained the main effect of CTI in the first period and the two-way interaction of PA coverage and forest cover index. The most simple models were the intercept only models, describing a scenario where none of our selected variables affected Δ CTI. The full sets of competing models are shown in Tables S5 & S6. Due to the strong collinearity of CTI in the first period and forest cover index in southern Finland, these two were not included into the same model to avoid erroneous interpretations of the effects of these variables. Thus, in addition to the intercept only model, the competing models explaining Δ CTI in the southern section had either CTI in the first period or forest cover index, alone and together with PA coverage within 100 km radius. Thus, the most complex model for southern Finland included only the two-way interaction between forest cover index and PA coverage within 100 km radius (Table S7).

Finally, the six competing models explaining Δ CTI in the three sections were evaluated by examining their AICc values (Tables S5–S7). The model with the lowest AICc value was chosen as the best to explain Δ CTI. However, if several models were ranked within Δ AICc ≤ 2 of the best ranked model, we chose the most parsimonious model for the model of inference, including fewer uninformative parameters than the other models within the Δ AICc ≤ 2 interval. A parameter was considered uninformative if the 85% confidence interval included zero (Arnold, 2010). If several top ranked models contained no uninformative parameters model averaging was performed under the R package MuMin (Barton, 2020), but we avoided model averaging of models with and without

interactions as this is not recommended (Cade, 2015).

We examined the distribution of residuals of all models explaining Δ CTI in all sections as to their adherence to the assumption of normality and found no deviations from this assumption. We also visually examined the presence of unexplained patterns in the residuals by plotting residuals of all models against fitted values and each explanatory variable. We detected no unexpected patterns. The presence of influential observations was examined by inspecting Cook's distances of the observations by plotting the model's standardized residuals against leverages using plot-function in R. These showed no values above 0.5, which would be potential outliers and would have merited detailed inspection. We also inspected visually the possible presence of spatial autocorrelation within the residuals by plotting the correlogram of residuals and distance of observations up to 500 km scale using spline.correlog function under the R package ncf (Zuur et al., 2009; Bjørnstad and Falck, 2001), and detected none.

We conducted a post-hoc analysis to assess if either warm- or cold-dwelling species were driving the significant connection between CTI change and PA coverage. This was done using jack-knife analyses, where one species at a time was removed from the data and the slope between CTI change and PA variable was compared to the original slope yielded when all species were present (Tayleur et al., 2016). The difference in slopes estimated the contribution of the removed species in the analyses (Tayleur et al., 2016). Species-specific contribution values were compared for each section between warm- and cold-dwelling species, having higher or lower STI values than an average of all the studied species, respectively. This comparison was made by using two-sampled *t*-test (wilcox.test function in R). All statistical analyses were performed in the R 3.5.3 software (R Core Development Team, 2019).

3. Results

Changes in CTI differed between sections ($F_{2,178} = 4.025$, $p = 0.020$) and were on average positive in all three areas: $+0.182 \pm 0.299$ (sd) in southern, $+0.330 \pm 0.270$ in central and $+0.288 \pm 0.294$ in northern section (Fig. 1b). A post hoc Tukey test revealed that the change in CTI was lower in southern than in central Finland ($p = 0.015$), but not between southern and northern ($p = 0.140$) nor central and northern Finland ($p = 0.674$).

We found that three models best explaining Δ CTI in northern section out of six were ranked within two AICc units (Table S5). The third ranked model contained one uninformative parameter, the two-way interaction between forest cover index and PA coverage. The 85% confidence interval for this parameter ranged from -0.030 to 0.004 ($b = -0.013 \pm 0.012$, $t = -1.106$, $p = 0.273$). The two models remaining did not show uninformative parameters (Table S8 & S9) and model averaging between the two was performed. It revealed that an increasing PA coverage was associated with a reduced change in CTI of the bird communities within PAs between the periods (Table 1, Fig. 2). Δ CTI was lower in PAs with higher CTI in the first period (Table 1). Forest cover index showed no significant effect on Δ CTI ($p = 0.132$; Table 1).

The top-ranked model for central Finland exhibited a difference of 2.22 AICc units to the second ranked model (Table S6) and was used as the model of inference for this section. In this model Δ CTI was explained by PA coverage, forest cover index and CTI in the first period ($F_{3,70} = 19.36$, $R^2 = 0.453$, $p < 0.0001$). Increasing PA coverage was associated with a reduced Δ CTI between the periods (Fig. 3a, Table 1), whereas higher values of the forest cover index were associated with increased Δ CTI (Fig. 3b, Table 1). CTI changed less between the periods inside PAs with higher CTI in the first period (Table 1).

Two of the models best explaining Δ CTI for the southern Finland exhibited AICc values within two units difference (Table S7). The second-ranked model contained an uninformative parameter. This parameter was PA coverage, which exhibited an 85% CI of -0.019 – 0.111 ($b = 0.047 \pm 0.045$, $t = 1.030$, $p = 0.308$). We therefore used the simplest and top-ranked model for inference about changes in CTI in the southern

Table 1

Summary table of the models explaining changes in community temperature index (CTI) between the two time periods of 1980–1999 and 2000–2015 within protected areas in northern, central and southern Finland. PA coverage represents the protected area coverage within a 100 km radius from the centre of the PA. The model estimates of northern Finland represent model averaging between two top ranked models, while estimates in central and southern Finland represent the top ranked model showing no uninformative parameters.

	Northern Finland				Central Finland				Southern Finland			
	b	SE	z	P	b	SE	t	P	b	SE	t	P
Intercept	3.405	0.788	4.222	<0.001	6.275	0.795	7.888	<0.001	4.766	1.074	4.438	<0.001
CTI _{1980–1999}	−0.253	0.067	3.686	<0.001	−0.478	0.063	−7.555	<0.001	−0.352	0.082	−4.271	<0.001
Forest cover index	0.132	0.177	0.737	0.461	0.401	0.117	3.417	0.001				
PA coverage	−0.013	0.003	3.939	<0.001	−0.049	0.012	−4.106	<0.001				

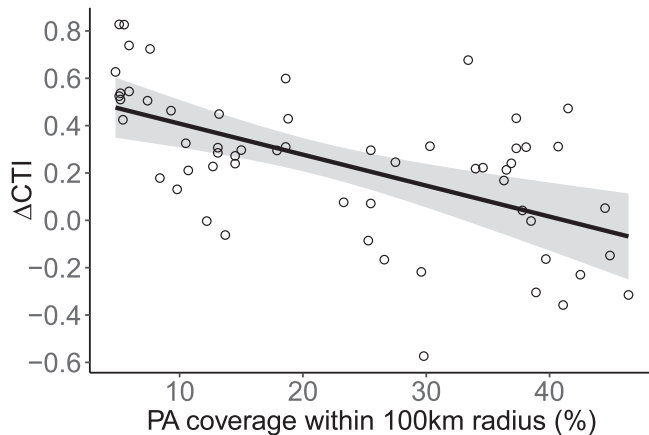


Fig. 2. Model estimates of changes in community temperature index (CTI) in protected areas of northern Finland between two periods of 1980–1999 and 2000–2015. The solid line represents the estimated effect of protected area coverage within 100 km radius on the Δ CTI in the top ranked model (Table S8), and the grey band represents the 95% confidence interval of this effect. Circles represent the partial residuals of observed values.

section. In this model, Δ CTI was only explained by CTI in the first period ($F_{1,74} = 18.24$, $R^2 = 0.280$, $p < 0.001$). Higher CTI in the first period was associated with reduced Δ CTI between the periods (Table 1).

We found no significant difference in the relative contributions of warm- versus cold-dwelling species in driving the observed CTI changes in northern ($t = 0.69$, $df = 113$, $p = 0.49$) or central Finland ($t = 0.63$, $df = 63.6$, $p = 0.53$). Essentially, both groups contributed similarly to the observed CTI changes in relation to the extent of PA coverage in these two sections.

4. Discussion

The results show that increasing PA coverage within a 100 km radius mitigated climate-driven community changes in PAs between the periods 1980–1999 and 2000–2015 in the northern and central sections. In northern Finland an increase of 10 percentage points in PA coverage reduced the Δ CTI by 0.13 units meaning that PA coverage of 45% had completely halted CTI increase. Increasing PA coverage with 10 percentage points in central Finland resulted in 0.44 units decrease in Δ CTI representing that protecting 13% of land cover would be needed to fully prevent increases in CTI. The results are in line with metapopulation theory, which states that communities are more resilient to environmental change when the landscape matrix contains a higher proportion of suitable, high quality habitat (Hanski, 1998). This is also supported by a study, which showed that bird populations were not affected by climate change in landscapes with only slight habitat loss (Northrup et al., 2019).

Although CTIs have generally increased within the PAs between the two periods under study, the communities within Finnish PAs exhibit higher densities of cold-dwelling species than neighbouring unprotected areas and are still today able to support communities with lower CTIs than those inhabiting unprotected lands in the 1970s–1980s (Santangeli et al., 2017). This suggests that despite cold-dwelling northern species are declining inside Finnish PAs (Virkkala and Rajasärkkä, 2011), these PAs are still able to alleviate impacts of climate-driven changes in bird communities and thus support our results. Further evidence of the high performance of PAs under climate change is provided by the ability of PAs to maintain higher bird abundances than unprotected areas at the trailing range margins of cold-dwelling species (Lehikoinen et al., 2019), to aid the persistence of northern species (Gillingham et al., 2015b) and facilitate the adaptation of high latitude species to a warming climate in the temperate biome (Gaüzère et al., 2016). Furthermore, PAs exhibit higher richness of species of conservation concern than unprotected land, and despite a warming climate this richness has remained higher for decades (Virkkala et al., 2014). Thereby there is strong evidence that PAs per se have the capacity to aid the persistence of diverse cold-

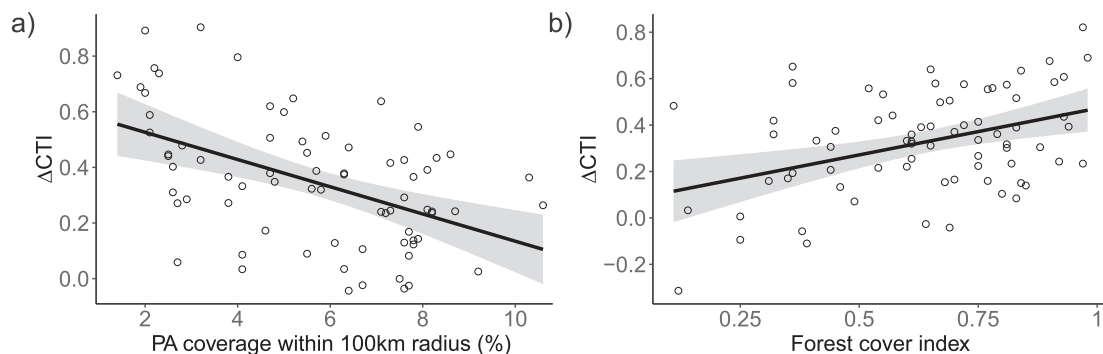


Fig. 3. Model estimates of changes in community temperature index (CTI) in protected areas in central Finland between two periods of 1980–1999 and 2000–2015. The solid lines represent the estimated effects of a) protected area coverage within 100 km radius from the center of PA and b) forest cover index, on Δ CTI (Table 1). The grey bands represent the 95% confidence interval of these effects, while circles represent the partial residuals of observed values.

dwelling species assemblies, at least in Northern Europe. Our novel results now show that such capacity of a single PA further increases with increasing proportions of PAs in the surrounding landscape. The latter can even fully compensate the climate-driven community changes.

We detected no significant differences in the contribution of cold- versus warm-dwelling species driving the observed slope between CTI change and PA coverage. This indicates that the PA network has a similarly strong effect on both groups (Tayleur et al., 2016), potentially meaning that high PA coverage reduces the decline of cold-dwelling species while simultaneously, and with similar extent, hinders the expansion of warm-dwelling species (Lehikoinen et al., 2019). Support for PAs' ability to hinder expansions of warm-dwelling species is presented in the marine environment, where PAs mitigate invasions by warm-dwelling fish species compared to nearby non-PA sites (Bates et al., 2014). Although this could suggest that such hindering effect can apply to PAs broadly, the resisting effect of expansions of warm-dwelling species in Finnish PAs could be linked with the habitat preference of this groups of species. Warm-dwelling species are more common in habitats found outside protected areas, such as cultural habitats (e.g. traditional agricultural biotopes) and early succession stage forests in active forestry use. Conversely, many cold-dwelling species, being boreal specialists, are more common in habitats found mainly inside PAs such as old growth forests and peatlands (Lehikoinen et al., 2019). Therefore, the cold-dwelling species may thrive in PAs where only few southern species are able to expand to (Lehikoinen et al., 2019).

Our findings highlight that the PA coverage within 100 km radius best explained the changes in community temperature index as compared to smaller radii or the size of the PA itself. This strongly suggests that the role of PAs in mitigating negative impacts of climate change should be investigated on a large spatial scale, and not only on the scale of e.g. single PAs. The importance of a well-connected PA network is supported by an empirical study on African Savannah birds, which shows that climatic conditions drive species to colonise new areas and that increased PA coverage facilitated such colonisation events and decreased local extinctions (Beale et al., 2013). Similarly, a Finnish study has revealed that increased proportions of old-growth boreal forests in the landscape matrix surrounding PAs correlate positively with the specialization of the avian community within the PAs. This suggests that PAs surrounded by intense logging activity are not able to maintain their species assemblage and levels of species abundances (Häkkinen et al., 2017). How widely applicable the findings are to other taxa and geographic regions remains unknown. There is a strong need to study the relationship between PA coverage and climate-driven community changes within PAs in different study systems and biomes. However, the above mentioned examples of PAs facilitating bird colonisations and reducing local extinctions in the African Savannah (Beale et al., 2013) and the ability of marine PAs to hinder fish community tropicalisation (Bates et al., 2014) provide some evidence that similar results to this study could be achieved in other regions and taxa.

We found no effect of PA coverage on community changes in southern Finland, where the PA coverage is clearly the lowest among the three studied sections (Fig. 1c). Although our analysis indicated that PA coverage within a 100 km radius was the best variable to describe the effect of PA coverage on Δ CTI, the overall PA coverage may be so low in this part of the country that detection of any statistically significant effect is difficult. This could mean that the PA network in southern Finland is too fragmented to support any detectable level of community resilience against climate change making these communities more fragile to climate-driven changes. This is partly supported by a study showing that current PA network in southern Finland fails to protect the future projected most suitable occurrence hotspots of forest bird species (Virkkala et al., 2013). Another recent study showed that avian densities inside Finnish PAs declined since 1980 in southern, but not in northern Finland (Virkkala et al., 2018). Furthermore, the low coverage of protected forests in southern Finland may not comprise suitable habitats for the northward expansions of southern forest species unrelated to the

boreal biome (Lehikoinen et al., 2019). Although the results from central and northern Finland support the need of increased PA coverage in southern Finland to counteract climate-driven community changes, there might be factors limiting the possibilities to do so. These include the small scaled private ownerships, high land price and intensive land management. Therefore the approaches to increase PA coverage may face economic, social and political barriers and be limited to small-scaled voluntary protection.

Increased availability of open habitats reduced changes in CTI in central Finland. This might at least partly be explained by an increased amount of open habitat creating structural heterogeneity compared to the rather homogeneous forest dominated landscapes of central Finland. Such fine-scale spatial heterogeneity is more likely to support higher species diversity than monotonic landscapes, due to the availability of different microclimates which help species adapt to climate change (Ackerly et al., 2010; Thomas and Gillingham, 2015).

Open habitats within PAs in southern and central Finland are more often open mires or half-open, sparsely wooded pine or spruce mires with poor tree growth rate (Metsähallitus, 2020). In southern and central Finland more than 75% of the original peatlands have been drained for forestry, agriculture and peat production purposes, and the remaining peatlands outside PAs show a high degree of degradation due to ditching and peat extraction (Fraixedás et al., 2017). The few open mire specialist species exhibit low STIs and their preferred habitats mainly remain inside PAs in southern and central Finland. Due to the draining efforts, open mires are not common in lower latitudes and the number of southern species colonising these habitats may be limited. Therefore, the species assemblages of open mires may have remained more stable as compared to those of forested PAs. In addition, many open habitat species, such as most waders, are northerly distributed and thus cold-adapted (Virkkala and Rajasärkkä, 2012; Santangeli et al., 2017) and their persistence in the less forested habitats in central Finland could mitigate the increases in CTI. This relation with low STIs and open habitat specialists is supported by the strong positive correlation of CTI in the first period and forest cover index in southern Finland, and therefore the effects of habitat composition could not be fully explored in this section.

To our knowledge, these results are among the first empirical evidence showing that climate-driven community changes can be mitigated by a high coverage of PAs in the landscape. The results support the projections that improvement of multispecies connectivity could be reached by increasing PA size and coverage in the landscape (Santini et al., 2016). PAs of the boreal biome are facing the highest velocities of climate change globally (Loarie et al., 2009), and bird populations in this biome have shifted northwards both outside and inside PAs (Lehikoinen and Virkkala, 2016; Virkkala et al., 2018). These highlight our findings of the ability of a comprehensive PA network at mitigating the community level changes under rapid climate change.

Despite the substantial alterations in species composition, high latitude PAs are projected to become important refuges for biodiversity under climate change (Berteaux et al., 2018), further emphasizing the role of boreal PA network. The role of PAs in facilitating range expansions (Gillingham et al., 2015a; Johnston et al., 2013; Thomas et al., 2012) is essential in supporting species and biodiversity in their potential adaptation to global warming. However, communities at high latitudes and altitudes are notoriously unable to retreat ceaselessly (Pacifi et al., 2017), underscoring the important role PAs play in retaining current communities and preventing major biodiversity losses. As the climate in Finland is projected to continue warming, the cold-dwelling species will face pressure to move outside Finland (Lehikoinen and Virkkala, 2016). While the Scandinavian mountains may provide further refugia for some of the cold-dwelling species to retract from the Finnish Lapland, the Arctic Sea prevents species retracting further north from Fennoscandia. Therefore, international conservation collaboration may be needed to ensure sufficient PA coverage performing as refuges for the retracting cold-dwelling species.

The discovered effect of an extensive PA network on decelerating the velocity of climate-driven community changes could further increase climate resilience by allowing time for adaptations to occur (Keeley et al., 2018). However on a global perspective, the present conservation efforts seem to be inadequate for the prevention of biodiversity loss (Butchart et al., 2010), and the goals to conserve and sustainably manage natural resources cannot be achieved under current trajectories (IPBES, 2019). Therefore, further expansions of PA networks are direly needed (CBD, 2018; Montesino Pouzols et al., 2014) to provide sufficient geographic and temporal coverage, avert further species declines and aid changing communities (Runge et al., 2015). Our results strongly indicate that expanding the PA coverage indeed increases the ability of communities to persist under changing climate and therefore support the international conservation policy strategies targeting PA network expansions for biodiversity conservation, at least under the conditions of this study system.

CRedit authorship contribution statement

Petteri Lehikoinen: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Visualization, Funding acquisition. **Maria Tiusanen:** Investigation, Methodology, Formal analysis, Writing - review & editing. **Andrea Santangeli:** Methodology, Data curation, Writing - review & editing, Funding acquisition. **Ari Rajasärkkä:** Resources, Data curation, Investigation, Writing - review & editing. **Kim Jaatinen:** Methodology, Writing - review & editing, Supervision. **Jari Valkama:** Writing - review & editing, Supervision. **Raimo Virkkala:** Writing - review & editing, Funding acquisition. **Aleksi Lehikoinen:** Conceptualization, Methodology, Investigation, Resources, Funding acquisition, Writing - review & editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108892>.

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